CHAPTER 18

Visual cortex organization in primates: theories of V3 and adjoining visual areas

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Abstract: After years of experimentation and substantial progress, there is still only limited agreement on how visual cortex in primates is organized, and what features of this organization are variable or stable across lines of primate phylogeny. Only three visual areas, V1, V2, and MT, are widely recognized as common to all primates, although there are certainly more. Here we consider various concepts of how the cortex along the outer border of V2 is organized. An early proposal was that this region is occupied by a V3 that is as wide and as long as V2, and represents the visual hemifield as a mirror image of V2. We refer to this notion as the classical V3 or V3-C. Another proposal is that only the dorsal half of V3-C exists, the half representing the lower visual quadrant, and thus the representation is incomplete (V3-I) by half. A version of this proposal is that V3-I is discontinuous, extremely thin in places, and highly variable across individuals, much as a vestigial or degenerate structure might be (V3-IF-incomplete and fragmented). A fourth proposal is that there is no V3. Many results suggest that a series of visual areas border V2, none of which has the characteristics of V3. Alternatively, the possibility exists that primate taxa differ with regard to visual areas bordering V2. Currently, much of the supporting evidence for a classical V3 comes from fMRI studies in humans, much of the evidence for a series of bordering areas comes from New World Monkeys and prosimian galagos, and much of the evidence for a V3-I or V3-IF comes from macaque monkeys. Possibly all these interpretations of visual cortex organization are valid, but each for only one of the major groups of primate evolution. Here, we suggest that none of these interpretations is correct, and propose instead that a modified V3 (V3-M) exists in a similar form in all primates. This V3-M is smaller and thinner than V3-C, discontinuous in the middle, but with comparable dorsal and ventral halves representing the lower and upper visual hemifields, respectively. Because the evidence for V3-M is limited, and it stems in part from our ongoing but incomplete comparative studies of V1 connections in primates, this suggestion requires further experimental evaluation and it remains tentative.

Introduction

Nearly all current investigators agree with the premise that neocortex is divided into a number of areas of differing functional roles. Each area is thought to be interconnected with several others, usually neighbors, to form processing networks or systems with serial and parallel components, and including feed forward, feedback, and lateral interconnections. Further components of this general agreement are that species vary in number of areas from few to many, that some basic areas are widely shared, and that closely related species are likely to share more areas (see Kaas, 1987).

While there is widespread agreement on the validity of this theoretical framework of brain function and organization, specific theories of how cortex is subdivided and interconnected have varied and continue to vary (see Kaas, 1995a, 1997b; Rosa, 1997). Since specific theories are highly valuable for interpreting and summarizing experimental and other observations, and they serve as guides for planning future research, it seems important to resolve the differ-
ences in current theories and move toward a theory that best accounts for the accumulating observations.

Our review focuses on the organization of the more caudal visual cortex that is involved in the early stages of cortical processing. These visual regions have been the most intensively studied, and thus there are more relevant observations and interpretations of observations for comment and comparison. Our review also considers evidence and theories based on all major lines of primate evolution for several reasons. First, such comparative studies can more reliably guide theories of the organization of the human brain (Kaas, 1997a). We agree that it is natural to be especially interested in the organization of visual cortex in humans, and the use of non-invasive brain imaging techniques, such as fMRI, have already revealed much about the organization of visual cortex in humans (see Tootell et al., 1996). Yet, most of us recognize the limitations as well as the advantages of studies on humans, and believe that information and theories obtained and developed from other primates can be very useful in helping us understand the human brain. Thus, conclusions about the organization of visual cortex in other primates, especially macaque monkeys, are commonly considered, and they greatly influence interpretations of data from humans. The focus on results from macaque monkeys is reasonable, in that our closest relatives, the great apes, are as inaccessible as humans for many types of studies. However, any predictions based on macaques alone should be treated with caution, given the 30 or so million years of independent evolution (Kay et al., 1997) of Old World monkeys and hominids (apes and humans). We feel that brain features that can be shown to be more widely distributed across primate taxa are more likely than variable features to be preserved in the human brain, and thus it is important to compare results across all studied primates (see Preuss and Kaas, 1999). Furthermore, proposed differences between primate species should be compatible with feasible courses of evolution, so that results and theories from one group of primates can be used to evaluate those from another group (see Kaas, 1997a). Of course, the different primates also offer various advantages in experimentally addressing questions about brain organization. In particular, the small, relatively smooth brains of many New World monkeys expose more visual areas on the surface where they are more accessible for study. Conclusions based on species where more compelling data can be obtained can be seen as applicable to other species if less compelling and incomplete data are supportive.

Given these reasons for comparing primates, and our conclusion that the organization of much of visual cortex is poorly understood, let us start by considering three visual areas that seem to exist in all primates.

Areas no longer in contention: V1, V2, and MT

Most investigators now agree that most or all primates have V1, V2, and MT (Fig. 1). There is widespread agreement on their boundaries, retinotopic organizations, major connections, and architectonic features (see Kaas, 1997b). Yet, this was not always so.

V1 or primary visual cortex appears to exist in all but possibly a few blind or nearly blind subterranean mammals (Kaas, 1980). Architectonically, V1 is one of the most distinctive of cortical areas, and thus it was the first identified subdivision of neocortex (see Gross, 1997). Yet, in early architectonic studies, another retrosplenial field was once misidentified as primary visual cortex, and even Brodmann (1909) mistook the thinner medial part of V1 (area 17) for another field (area 18) in rodents. More recently, some investigators have wrongly concluded that the more differentiated V1 of cats and primates is not the same field as V1 in hedgehogs and rats (see Kaas, 1987).

The second visual area, V2, is also an area that likely exists in all mammals except those with a reduced visual system (see Catania et al., 1999). Yet, interpretations of the size, location, retinotopic organization, and even the existence of V2 have varied. Most notably, many investigators conclude that the lateral border of V1 in rats and several other rodents consists of a series of small areas rather than V2, while others consider the proposed areas as subdivisions of V2 (see, Kaas et al., 1988; Rosa and Krubitzer, 1999). Largely because a characteristic banding pattern exists in histological preparations of V2 of most primates (see Krubitzer and Kaas, 1989; Roe and Ts’o, 1997), there is now good agreement on the extent and location of V2 in these mammals.
Fig. 1. Our current proposal for how visual cortex is subdivided into areas in primates shown on an unfolded view of neocortex in a New World monkey (marmoset). More established areas are outlined, others are indicated, while other proposed areas are not included. Outlined areas include primary visual cortex (V1), the second visual area (V2), dorsal and ventral V3 (V3d and V3v) as divisions of a redefined third visual area (V3), the dorso-medial area (DM), the middle temporal area (MT), the middle temporal crescent (MTC), the medial superior temporal area (MST), the dorsal and ventral divisions of the fundal area of the superior temporal sulcus (FSTD and FSTV), and caudal and rostral (DLC and DLR) divisions of the dorso-lateral area (DLL). Representations of the upper (+) and lower (−) visual quadrants are indicated for some of the visual areas. For some visual areas the zero horizontal (hollow circles) and the zero vertical (hollow squares) meridians are marked. Filled circles represent estimated location of foveal vision in DM and MT. The ventral anterior (VA), inferior temporal (IT), superior temporal sulcus (STS) and posterior parietal (PP) visual regions are also indicated. For reference, the somatosensory areas, area 3b or primary somatosensory cortex (S1), the second somatosensory area (S2), the parietal ventral somatosensory area (PV), and the auditory core (A) are also outlined. LS, lateral sulcus. Shaded regions are parts of cortex that have been exposed by unfolding. Arrows indicate medial (M) and Rostral (R) directions.

The middle temporal visual area, MT (also called the visual area of the superior temporal sulcus, the motion area, or V5), was first identified in owl monkeys as a densely myelinated oval of cortex with a systematic representation of the contralateral visual hemifield (Allman and Kaas, 1971). The approximate region of cortex was known to be responsive to visual stimuli (Woolsey et al., 1955), and to receive projections from V1 (Kuyper et al., 1965), but no MT-like area existed in early proposals of cortical organization based on architecture. Furthermore, while connections between V1 and MT are now recognized as retinotopically matched, various other concepts have been proposed. Initially, projections to the region were thought to be convergent, without a topographic pattern (Zeki, 1971) or convergent and to a larger ring-like area that circled V1 at a distance (Cragg, 1969). Another interpretation was that the V1 projection zones in the middle of the temporal lobes of owl monkeys and macaques were not to the same area (Zeki, 1980). The consensus opinion now is that MT exists as a densely myelinated V1 oval in the same relative position and with roughly topographic interconnections with V1 in all primates.

While V1 and V2 are areas that exist in most mammals, it is uncertain if MT exists in mammals other than primates. Since MT seems to be present in all primates, it is logical to assume that MT emerged with the first primates or even earlier. Because the
Clare-Bishop region or area of cats has several of the features of MT in primates, including a representation of the visual hemifield, projections from V1, and a location displaced from the V1 border towards the upper temporal lobe, the Clare-Bishop area has often been considered to be a homologue of MT (e.g. Payne, 1993; Creutzfeldt, 1993). If the Clare-Bishop area and MT are homologous, one would expect to find an MT in many of the extant mammals that have descended from the common ancestors of cats and primates. Yet, there is little evidence for an MT-like area in other mammals. V1 projections to an oval of cortex lateral to V2 have been reported in several mammals including squirrels (Kaas et al., 1988) and tree shrews (Lyon et al., 1998). Admittedly, these regions of cortex resemble MT in having inputs from V1, in having a crude map of the visual hemifield, and perhaps in other ways, but they are located next to V2 rather than displaced into the temporal lobe. However, an MT-like area, slightly displaced from the V2 border, has been referred to as MT in megabats (Rosa, 1999). Possibly MT in primates and the Clare-Bishop region in cats both stem from an older area with V1 inputs that was independently displaced from the V2 border in lines of descent leading to these present-day mammals (Kaas, 1995b). Alternatively, MT and the Clare-Bishop region could be independent products of the evolution of complex visual systems with many cortical areas. Such issues of homology cannot be easily settled by studying cats and primates alone. A broader, cladistic approach is required (Harvey and Pagel, 1991).

Our purpose in mentioning all these various interpretations of visual cortex organizations is not to devalue the serious efforts of previous researchers, but to emphasize how various interpretations typically are supportable, and that, with the accumulation of additional evidence, widespread agreements sometimes emerge. In the next section, we discuss views of how visual cortex along the outer border of V2 is organized, with the expectation that if we make differences in opinion more explicit, more research and progress toward a consensus view will occur.

**Do primates have a V3?**

With the evidence for a third visual area, V-III, in cats (see Hubel and Wiesel, 1965; we use the terms V-III in cats and V3 in primates to distinguish visual areas of the same name in the two taxonomic groups), it was logical to look for evidence for a V3 in primates. In cats, V-III has been described as a visual area along the complete length of the outer border of V2 with the width of V2 and a retinotopic organization that mirrors that of V2 (Tusa et al., 1979; Albus and Beckmann, 1980). V-III also receives retinotopically matched projections from V1 and V2. Indeed, early proposals of visual cortex organizations based on studies of V1 projections in macaque monkeys (Cragg, 1969; Zeki, 1969) included a V3 (then called ‘area 19’ or V-III) that had all of these characteristics of V-III of cats. We refer to this original depiction as the classical V3 or V3-C (Fig. 2A).

Since those early anatomical studies, evidence has accumulated to support several greatly modified concepts of V3. The modifications emerged in steps, with the most radical departure being the concept that only the dorsal half of V3 is V3, with the ventral half being another visual area, the ventroposterior visual area, VP (see Van Essen, 1985). We refer to this concept as V3-I because V3 is incomplete (representing only the lower visual quadrant) or, as previously noted (Kaas, 1996), improbable because it lacks an upper quadrant representation. Other modifications emerged so that a recent depiction is of a discontinuous remnant of dorsal V3 (Fig. 2B) that is as narrow as 1 mm in places, so limited in extent that it would not seem to be able to even represent all of the lower quadrant, and extremely variable in shape across individual macaque monkeys (Van Essen et al., 1986). This incomplete and fragmented V3 (V3-IF) is just a fraction of what one might expect for a visual area. The proposed variability in shape and extent across individuals, and the gross incompleteness of the representation suggest a visual area that is vestigial, one that has lost its functions and has been allowed to drift and degenerate without positive selection in evolution.

There were logical reasons for making this remarkable change in the proposed form of V3. First, the evidence for the classical V3 was based on assumptions about total projection patterns that were only partly known. Most of the accessible dorsal portion of V1 in macaque monkeys represents central and paracentral vision of the lower visual quadrant,
Fig. 2. Different concepts of V3 and visual cortex organization in primates. (A) In early and more classical or traditional views, V3 was seen as a third level of processing, equal in size and importance to V2. V2 and classical V3 (V3-C) were seen as successive ring-like areas around most of V1, with their common border formed by a representation of the horizontal meridian (HM; hollow circles), and the outer border of V3 by the vertical meridian. Both V2 and V3-C were thought to receive retinotopically congruent inputs from V1 in mirror reversal patterns. Thus, a region on the horizontal meridian in V1 (a) would project to the border regions of V2 and V3, both dorsally and ventrally due to the ‘split’ representation of the horizontal meridian. Locations centered in the representations of the lower (bl) and upper (bu) visual quadrants in V1 would project to the middle of dorsal or ventral V2 and V3, respectively. Finally, locations along the outer border of V1 would project locally to V2 and to the outer border of V3 (cl and cu). Note the representation of the fovea (F). (B) Subsequently, V3 was viewed as incomplete (V3-I), representing only the lower visual quadrant, or incomplete and fragmented (V3-IF), being separated into a larger part for more central lower field vision and a smaller part for more peripheral lower field vision. The former territory of ventral V3 was considered to be another visual area, the ventroposterior area (VP). According to this scheme, V1 would project in a retinotopic pattern to both dorsal and ventral V2, but only to dorsal V3. Alternatively, some theories retained a region of cortex for a ventral V3, but presumably this ventral V3 lacked V1 inputs and it differed from dorsal V3 in other ways. (C) Other investigators held that there was no V3. Projections from V1 to dorsomedial cortex along outer V2 were considered to be to a dorsomedial visual area (DM) rather than V3. Note that this theory predicts that all parts of V1 will project to the DM region, while the theory of an incomplete V3 (V3-I) predicts the existence of projections only from dorsal V1. (D) Our current proposal is that V3 exists as a complete representation that is nevertheless split into separate dorsal and ventral halves, each considerably smaller than the corresponding halves of classical V3 (V3-C). The dorsal half of this modified V3 (V3d-M) gets inputs from dorsal V1, while the ventral half (V3v-M) gets inputs from ventral V1. In addition, DM remains as a visual area with inputs from all parts of V1. In reduced size and location, this V3-M resembles the discontinuous and smaller V3 of Ungerleider and Desimone (1986).
and lesions and injections in this cortex did reveal projections to MT, dorsal V2, and cortex just outside the rostral border of dorsal V2. The terminations in cortex just rostral to dorsal V2 provided evidence for a V3, and it was reasonable to assume that ventral V1, representing the upper visual quadrant, would project to ventral V2 and cortex just rostral to ventral V2, providing missing evidence for a ventral V3. However, subsequent studies of V1 projections in macaques (e.g. Weller and Kaas, 1983; Van Essen et al., 1986) and other monkeys (e.g. Krubitzer and Kaas, 1993) failed to provide clear evidence for a ventral V3 (also see Newsome et al., 1986; Felleman et al., 1997). Furthermore, the response properties of neurons in the region of ventral V3 seemed to differ from those of dorsal V3 (Burkhalter and Van Essen, 1986; Burkhalter et al., 1986). Thus, there was no compelling evidence for a ventral V3, and the concept of V3 was modified by some of these investigators to exclude a ventral V3. The region of ventral V3 was assigned to another visual area, the ventroposterior area or VP (Newsome et al., 1986). However, others retained the concept of a more classical V3, with ventral and dorsal halves, but separated the halves in the region of central vision (see Ungerleider and Desimone, 1986). The ventral half of V3 would be ‘deprived’ of V1 input (Fig. 2B).

A further modification in the concept of V3 came from a careful analysis of the myeloarchitecture of the region (Van Essen et al., 1986). V3 was associated with a densely myelinated strip of cortex along the outer border of V2, and this strip appeared only dorsally, was narrow (1–3 mm in width), discontinuous, and variable. We refer to this as an incomplete, fragmented V3 or V3-IF (Fig. 2B). Further support for a discontinuous, narrow dorsal V3 came from a microelectrode mapping study of the region (Gattas et al., 1988). The concepts of V3-I and V3-IF differ so much from those of V-III in cats or V3-C in monkeys that one wonders if the designation ‘V3’ is more confusing than descriptive.

Arguments for a third major alternative were presented in the early microelectrode mapping studies of extrastriate cortex organization in owl monkeys by Allman and Kaas (e.g. Allman and Kaas, 1974, 1975, 1976). Although a cat-like classical V3 was expected at the time, no convincing evidence for such an area was found. Instead, the outer border of V2 seemed to be formed by a series of small visual areas. The proposal that V2 is bordered by a series of visual areas has been extended to include other primates (see Kaas, 1997b).

Originally, it appeared that V1 projections in New World monkeys were only to V1 and MT (Tigges et al., 1973; Spatz, 1977), but when more sensitive tracing methods were used, sparse projections to the approximate region of dorsal V3 were revealed as well (Lin et al., 1982). However, these projections were attributed to the dorsomedial visual area, DM, rather than to dorsal V3 (Fig. 2C). Further support for this interpretation of V1 projections followed, when a number of studies indicated that both V1 and V2 project in a topographic pattern to a zone of densely myelinated cortex just rostral to dorsal V2 in prosimian galagos, New World monkeys, and Old World monkeys (Krubitzer and Kaas, 1993; Steniewska and Kaas, 1996; Beck and Kaas, 1998a,b, 1999). The evidence that projections originally attributed to dorsal V3 were really part of a more extensive pattern of V1 projections to another visual area, DM, seemed to remove the most compelling evidence for V3. If V1 projects to neither a ventral nor a dorsal V3, then the argument for a V3 at all would seem to be reduced to the evidence that cortex immediately rostral to dorsal V2 largely represents the lower visual quadrant, and cortex immediately rostral to ventral V2 largely represents the upper visual quadrant (e.g. Sereno et al., 1994, 1995; DeYoe et al., 1996). However, such data are open to the alternative interpretation of a series of bordering visual areas with largely matching or congruent retinotopic borders with V2 (see Sereno, 1998; Rosa, 1997).

Given these alternatives, some might be tempted to conclude that primate species differ in organization of extrastriate cortex along the outer border of V2 (e.g. Sereno, 1998). Current depictions of the retinotopic organization of human visual cortex as derived from fMRI studies typically contain a broad, classical V3 (e.g. Shipp et al., 1995) or a broad dorsal V3 and a broad ventral counterpart, a ventroposterior area with a retinotopy much like one would expect for the ventral half of classical V3 (e.g. Tootell et al., 1997). Much of the evidence for a series of visual areas bordering V2 comes from New World monkeys and prosimians, while arguments for
a reduced, fragmented dorsal V3 stem only from results obtained from Old World monkeys. Possibly humans have a classical V3, macaques have an incomplete, fragmented V3, and other primates totally lack a V3. This conclusion would encompass most of the experimental observations, but it would require a very improbable evolutionary scenario.

**A proposal for a modified V3 as an area common to primates**

A fourth possibility for the interpretation of the organization of visual cortex immediately surrounding V2 is suggested by the results of our ongoing research on the connections of V1 in primates (Lyon and Kaas, 2000). While these studies are incomplete, and the evidence is limited, the results support an interpretation of the projection patterns of V1 to extrastriate cortex that may apply to all primates (Fig. 2D). Our proposal is based on the following observations and conclusions. First, considerable evidence now indicates that all parts of V1 project to DM, a visual area just rostral to the middle of dorsal V2 (see Beck and Kaas, 1999). The location of this projection zone appears to be similar in all studied primates. All of our recent results are consistent with the conclusion that DM is a target of V1 projections.

Second, dorsal V1 also projects, usually less densely, to a narrow strip of cortex we now locate between DM and V2, but was formerly included in either V2 or DM. Since the V1 projections to DM are immediately adjacent to those to V3d, it could be very difficult to distinguish the V3d terminations from DM terminations. However, the use of surface-view sections of flattened visual cortex convinced us that injections in dorsal V1 produced two distinct foci of terminations, one in cortex we now identify as V3d, and one in DM. We suggest that previous descriptions of projections from dorsal V1 to a dorsal V3 may have included terminations in DM, V3d, or even outer V2. Given the denser projections to DM, it seems likely that the more obvious DM terminations were most often detected and attributed to V3. While the full extent of V3d is not yet clear, it does appear from connection patterns and the architectonic features to be a very narrow field that includes only part of the border of dorsal V2.

Third, as previously reported, ventral V1 also projects dorsally to DM, to complete the retinotopic representation in DM. However, our results indicate that ventral V1 also projects ventrally, but less densely, to a ventral V3 along the outer border of ventral V2. This proposed V3v exactly matches V3d in its narrow width and limited extent, but it represents the upper visual quadrant while V3d represents the lower visual quadrant. Although separated by a portion of dorsolateral cortex along the representation of central vision in V2, the two halves of V3 both get V1 inputs and they appear to be parts of the same visual area.

Our conclusion that ventral V1 projects to a ventral half of V3 is critically important for any firm acceptance of the concept of a V3 as an area common to primates. Yet our evidence is limited to results obtained from injections in New World monkeys and galagos (Lyon and Kaas, 2000) and thus our proposal should remain tentative. The lack of evidence for such a ventral projection in previous studies remains a concern, but there are several reasons why such projections may have been missed. Most importantly, the projections are sparse, and sparse projections are not always revealed. Injections in ventral V1 may have been small relative to those in dorsal V1 in order to avoid contamination of dorsal V1. Furthermore, the projections of the less accessible ventral half of V1 have been less often studied. In addition, even the projections to dorsal V3 may have been commonly missed, and the denser projections of dorsal V1 to DM may have been spuriously attributed to V3d. Finally, V3v and V3d are narrow, so that it would be difficult to distinguish terminations in V3 near the outer border of V2 from those in V2. Projections just beyond the outer border of V2 may have been assigned to V2. Thus, the evidence for V1 projections to either V3v or V3d has been questionable.

Our proposal of a redefined, narrow V3 raises the issue of how to interpret the evidence from previous studies of V3 connections, neuron response properties, and architecture. Clearly, we need ways of distinguishing conclusions that have been based solely on results from V3 and results contaminated by including parts of DM or other visual areas. A related question is how V3 functions in the visual system. This V3-M (Fig. 2D) is about half the width
of V2 and fails to border central V2 and possibly the ends of V2. Thus, V3-M is significantly smaller than V2, and it receives less V1 input than V2, MT or DM. Obviously, this narrow, split V3-M cannot have the classically proposed role for V3 as the third major stage of visual processing, equal in importance to V2. Instead, we see V3 as one of several distribution targets of V1, with V2, MT and DM each receiving more of the output, and other areas receiving some of the V1 outputs (see Casagrande and Kaas, 1994). Furthermore, V3-M would contain compressed representations of the visual quadrants, and this would restrict some functions. In some sense, V3 may act as a transition zone between the retinotopy of V2 and the retinotopies of the ring of bordering areas. In marmosets, we have evidence that both dorsal and ventral portions of V3 get inputs from MT as well as V1. The MT inputs suggest that V3 is functionally aligned with the dorsal stream of processing (Ungerleider and Mishkin, 1982) related to spatial aspects of vision.

The possibility that all primates have a V3, albeit not a classical V3, raises the possibility that V3 in primates and V-III in cats are homologous subdivisions of visual cortex, as often suggested (e.g. Albus and Beckmann, 1980; Rosenquist, 1985; Creutzfeldt, 1993; Payne, 1993). A cladistic analysis of the organization of visual cortex in studied mammals casts doubt on this attractive assumption. If carnivores and primates have inherited a V3 from a common ancestor, then members of sister orders of mammals should have a V3 as well. So far, there is little evidence that this is the case. For example, squirrels (Kaas et al., 1988) and other rodents (Rosa and Krubitzer, 1999), as well as tree shrews (Sesma et al., 1984; Lyon et al., 1998) do not appear to have a V3. Yet, new evidence may be forthcoming, and the interpretation of data on the organization of visual cortex is surprisingly difficult. Thus, the assumption of a homology between V-III of cats and V3 of primates is at the expense of the caudal part of DM and adjoining fields (Fig. 3). This DM remains as a possibly smaller visual area, somewhat displaced from the V2 border, but containing a complete representation of the contralateral visual hemifield and having inputs from all parts of V1 and V2. The way the visual field is represented in DM can be surmised from the input patterns (Krubitzer and Kaas, 1993; Beck and Kaas, 1998a,b, 1999; Lyon and Kaas, 2000) and from previous studies of retinotopy (Allman and Kaas, 1975; Krubitzer and Kaas, 1993; Rosa and Schmid, 1995). While the retinotopic organization of DM remains somewhat uncertain in detail, the representation of the lower visual quadrant is largely along the V3d border, and the representation of the upper visual quadrant is largely rostral and more lateral (Fig. 1). The representation of central vision may be more lateral than originally depicted (see Allman and Kaas, 1975), and peripheral vision is medial. The proposal that the representation of the upper visual quadrant is split in DM, with more central vision represented rostro-caudally and more peripheral vision caudomedially along the ventral border remains a possibility (Rosa and Schmid, 1995; Rosa, 1997) but further studies combining connectional, architectonic, and microelectrode mapping approaches would be useful. If the outer border of V3d represents the zero vertical meridian of the lower quadrant, as proposed, then we would expect adjoining parts of DM to match along the zero vertical meridian.

Our modified DM continues to occupy cortex assigned to other visual areas in other proposals, but exactly what other areas remains uncertain (Fig. 3). Clearly modified DM would overlap with an outer portion of classical V3, but with little or none of the incomplete, narrow V3 of later proposals (Fig. 2). Much of DM may correspond to V3A (see Krubitzer and Kaas, 1993; Beck and Kaas, 1999). V3A was described as a visual area adjoining parts of the dorsal border of V3 in macaque monkeys (Zeki, 1978). Another possibility (see Rosa, 1997) is that DM overlaps partly or largely with another parietal-occipital visual area or PO (Colby et al., 1988). However, PO in macaques was originally thought to be the homologue of the medial visual area, M, first described in owl monkeys (Allman and Kaas, 1976). More recently a ‘V6’ has been described in the
Fig. 3. Some unresolved issues of visual cortex organization. Borders for visual areas described in Fig. 1 (V1, V2, V3d, V3v, DM, M, DLc, DLr, VA, MT, MTC, MST, and FST) are shown on a diagram depicting proposed areas of visual cortex organization of Old World monkeys, based on previous diagrams (see Kaas, 1997b) and recent results from New World monkeys (Lyon and Kaas, 2000). Locations of area 7a and visual areas of the intraparietal sulcus, the medial intraparietal (MIP), ventral intraparietal (VIP), lateral intraparietal (LIP), and anterior intraparietal (AIP) areas, are based on other reports (see Rosa, 1997).

The inclusion of a V3d displaces DM from the dorsal half of the V2 border (see Figs. 1 and 2D) and puts more of DM in a position very similar to area V3A of macaques and humans. The region rostral to DM shown as gray and bordered by a dashed line indicates the uncertainty as to where visual areas V6 and V6A (Galletti et al., 1995, 1999) fit within our current theory of primate visual cortex organization. It is possible that V6 may partially or completely overlap with DM and/or V3A. Furthermore, area V6A shows functional characteristics similar to those described for area MIP, namely visually guided reaching (Johnson et al., 1996). Other issues concern the similarity of visual areas M and POd (the surviving division of the parieto-occipital area) and whether these two regions actually represent the same cortical area. The dorsointermediate area (DI) is shown as a possible candidate for the region of visual cortex between DM and DL, but without any certainty of its borders. Inferior temporal visual cortex (IT), and somatosensory cortical areas 5 and 7b are shown for reference.

approximate location of DM in macaque monkeys (Galletti et al., 1995, 1999), and V6 may occupy much of the territory of DM. Other visual areas such as the posterior intra-parietal area, PIP, have been proposed for the region (Felleman and Van Essen, 1991). Thus, there is much uncertainty about how to divide this region into areas and how to name them.

This uncertainty stems in part from the difficulties in exploring cortex buried in the region where the lunate, intraparietal, and parieto-occipital sulci converge in macaque monkeys. Our present studies have focussed on marmoset monkeys where the region is exposed on the dorsolateral surface of the cerebral hemisphere, and none of these fissures exist. To the extent that visual cortex between New and Old World monkeys is subdivided into areas in a similar manner, it seems much more productive to determine the basic organization in such New World monkeys. Of course, a plan of organization developed from data on New World monkeys would need to be evaluated for applicability to Old World monkeys, but this could be done more reliably when highly specific hypotheses exist. For example, we propose that connection patterns with V1 and V2 can be used to reliably identify and delimit DM in macaques.

Of course it remains possible that the organization of extrastriate cortex will be found to differ significantly in New and Old World monkeys, even in the DM region. If this turns out to be the case, then humans and macaques may also differ and we should be very cautious about using results from macaque monkeys to model the organization of human visual cortex. However, much evidence supports the view that all primates share a number of visual areas. The evidence that all primates have a V1, V2, and MT is quite convincing. We would add V3-M, DM, DL and M to the list.

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